

Consequences of fundamental physical and dimensional constraints on ecosystems

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We perform the first bottom up analysis of an idealized ecosystem using Buckingham's Pi theorem. Our analysis requires only three assumptions, (i) that the ecosystem is in a dynamically balanced steady state, (ii) that some (non-unique) method exists that can differentiate different functional groups of individuals within the ecosystem and (iii) that these functional groups are connected to each other by the flow of resource. The expression that we obtain relates the level of complexity that the ecosystem can support to intrinsic macroscopic variables such as density, diversity and characteristic length scales for foraging or dispersal, and extrinsic macroscopic variables such as habitat size and the rate of supply of resource. This expression relates these macroscopic variables to each other, generating commonly observed macroecological patterns. Since we do not require any details of the ecosystem function to obtain these broad macroecological patterns this may explain why they are ubiquitous. Departures from our relationship may indicate that the ecosystem is in a state of rapid change, i.e., abundance or diversity explosion or collapse. Our result provides normalised variables that can be used to isolate the trend in one ecosystem variable from another, providing a new method for isolating macroecological patterns in data. Quite generally, a dimensionless control parameter for ecosystem complexity emerges from our dimensional analysis. This, we suggest, will be a control parameter in dynamical models for ecosystems based on energy flow and conservation and will order the emergent behaviour of these models.

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I. INTRODUCTION

The rapid increase in the availability of large-scale ecological data, and the recent rise of the discipline of macroecology [1, 2] have simultaneously increased our knowledge of global patterns and stimulated the search for the underlying processes that determine them (see [3]). Examples of the large-scale, macroecological, patterns [4] to have emerged from empirical analyses include the species-area and the species-latitude relationships, and trends in density and diversity with body size. These are broad scale patterns and generalised rules rather than mechanistic processes, and a range of theories have been proposed to explain why these patterns emerge. This has led to the development of a perspective in which the detailed biological characteristics of the species (traits) do not determine their abundance and that the processes affecting community structure can be considered as neutral [5–7], see also [8, 9]. The fact that these patterns are both approximate and ubiquitous, suggests that they do not reflect the details of how ecosystems operate, rather that they emerge from underlying general constraints.

Rather than exploiting statistical constraints, as in maximum entropy inference [6, 10–12], we focus on *physical and dimensional* constraints and how these relate the level of complexity that the ecosystem can support, to intrinsic variables such as density, diversity and characteristic lengthscales for foraging or dispersal, and extrin-

sic variables such as habitat size and the rate of supply of resource. Any model or function that relates physical quantities has a fundamental property; that the interdependencies which it captures must be independent of the units in which the quantities are measured, that is, it must be expressible completely in dimensionless parameters [13–15]. As a consequence, if we observe a particular set of ecosystem variables, since these variables possess physical dimensions (mass, length, time) there are dimensional constraints on the relationships that can exist between them. Importantly, formal dimensional analysis yields these *dimensional* constraints without detailed knowledge of the functioning of the ecosystem; it does not specify a unique relationship between the variables. We can obtain this if in addition there are known *physical* constraints, such as conservation principles. The physical constraint that will be central to this paper is that of an ecosystem which adapts dynamically to changes in external parameters to maintain a balance between the rate of uptake and of utilization of resources taken over the ecosystem as a whole. The concept of ecosystems which compensate dynamically to remain in homeostasis has been explored by [16, 17] but not developed using dimensional analysis.

In this paper we will only require three key assumptions, (i) that the ecosystem is in a dynamically balanced steady state, (ii) that some (non-unique) method of observation can differentiate different functional groups of individuals within the ecosystem and (iii) that these functional groups are connected to each other by the flow of resource. This will yield an expression that relates the level of complexity in the ecosystem as quantified by (ii) to its characteristic intrinsic and extrinsic vari-

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ables. This expression constrains the relationships that can exist between these (dimensional) ecosystem variables which we will see is reflected in overall macroecological trends that are observed. Further, we obtain the relationship between these trends. At minimum this leads to the dimensionless, or normalised variables that need to be constructed to isolate variation in one ecosystem variable from another; this provides a new method for isolating macroecological trends. At maximum, we obtain a dimensionless control parameter and relate it to the level of complexity that the ecosystem can support, which points towards ‘thresholds for life’, that is, a parametrization of the minimum level of complexity that a dynamically balanced ecosystem can support.

Process based models of ecosystems that aim to predict macroecological patterns tend to fall into two approaches. The first of these relates area, diversity and abundance by means of models for dispersal, occupancy and coexistence/competition and speciation in physical space (see e.g. [3, 7, 18, 19]). The second relates abundance, body mass and metabolic rate by means of models and constraints for the availability and flow of resource ([20], see the review of [21]). The relationship that we obtain here links the key parameters of both these approaches, suggesting a synthesis of them.

II. FORMAL DIMENSIONAL ANALYSIS AND A BOTTOM UP- APPROACH TO AN ECOSYSTEM

We will build our understanding by first considering the simplest possible idealized ecosystem and then successively increasing the level of complexity; at each stage, additional variables are introduced. Our approach is to use formal dimensional analysis at each stage to find the constraints that act on this general description of an ecosystem. Importantly, we seek to describe an ‘observed macroscopic ecosystem’, that is, the variables that we will ultimately identify include observed intrinsic properties such as density, diversity, body size, and metabolic rate. Introducing progressively more specific detail inevitably introduces more characteristic variables- this procedure could be taken further to explore specific detailed ecosystem models by the input of more detailed ecosystem functional properties into the dimensional analysis. Our aim here is rather to explore the ecosystem constraints that emerge for the minimum set of assumptions and model inputs.

Any model for a physical system that depends upon V variables Q_1, Q_2, \dots, Q_V must provide a function F that relates them: $F(Q_1, Q_2, \dots, Q_V) = C$ where C is some dimensionless constant [15]. The physical system that we discuss here is that which captures general physical aspects of ecosystem function, specifically the uptake and utilization of resource. The essential idea of formal dimensional analysis is that this function can only depend upon dimensionless parameters $\Pi_1, \Pi_2, \dots, \Pi_M$ so that $F = F(\Pi_1, \Pi_2, \dots, \Pi_M)$ only. These dimensionless pa-

rameters $\Pi_{1..M}(Q_{1..V})$ are formed directly from the variables Q_1, Q_2, \dots, Q_V . Formal dimensional analysis as in Buckingham’s Π theorem ([13–15], see also [22]) is simply the process to obtain these dimensionless groups of variables. If one then has additional information about the system, such as a conservation property, the $\Pi_{1..M}(Q_{1..V})$ can be related to each other to make F explicit. If the V relevant variables $Q_{1..V}$ are expressed in W physical dimensions (i.e. mass, length, time) then from [13] there will be at least $M = V - W$ dimensionless parameters or groups $\Pi_{1..M}(Q_{1..V})$ which we now progressively identify.

A. One kind of uniformly distributed single cell organism.

The ecosystem is composed entirely of single cell organisms that are of uniform type: they have the same function and structure and same typical metabolic rate R , dimensions $[M][L]^2[T]^{-3}$. They are uniformly distributed in a habitat of size L in D dimensions with density n , dimensions $[L]^{-D}$. The available resource (sunlight) is delivered at rate P per unit area, dimensions $[M][T]^{-3}$ and the (dimensionless) fraction α taken up by the ecosystem is a constant. There are 5 variables (R, L, P, α, n) and 3 physical dimensions (mass $[M]$, length $[L]$, time $[T]$) so we have 2 parameters (dimensionless groups) which are

$$\Pi_1 = \frac{\alpha PL^2}{R}, \Pi_2 = nL^D \quad (1)$$

These are related by the physical constraint that the system is in dynamical balance so that the rate at which energy is taken up over the ecosystem is the rate at which it is utilized, so that:

$$\frac{\alpha PL^2}{R} = nL^D \quad (2)$$

which is $\Pi_1 = \Pi_2$. This expression simply tracks the flow of energy into and through the ecosystem- it assumes that all other processes necessary for the ecosystem to function, such as the recycling of resources such as Nitrogen, occur. Introducing a typical metabolic rate for the single cell organisms has fixed an energetic minimum threshold for life which is $\Pi_1 = 1$, that is, one cell in the habitat (one cell ecosystem).

B. More than one kind of single cell organism.

We next consider single cell organisms that can be differentiated from each other, either by their function or their structure, or both. These would represent distinct types or species and different methods for categorizing and distinguishing individuals will yield different sets of species. What will follow will be independent of the precise details of this differentiation method, we only need assume that such a differentiation is now possible. In

the ecosystem there are S types (species) and there is a species label $k = 1..S$, the density of the k^{th} species is $n(k)$. We can always define an average density of the single cell organisms:

$$\bar{n} = \langle n(k) \rangle_k = \frac{1}{S} \sum_{k=1}^S n(k) \quad (3)$$

so that the variable n in (1) is now replaced by \bar{n} and $\Pi_2 = \bar{n}L^D$. The additional variable S is dimensionless; so that we now have 6 variables and 3 dimensions, and so 3 dimensionless parameters with $\Pi_3 = S$. These are again related by the physical constraint that the system is in dynamical balance:

$$\frac{\alpha PL^2}{R} = \sum_{k=1}^S n(k)L^D = \bar{n}SL^D \quad (4)$$

Expression (4) now encapsulates the idea of primary producers- one or more of the species is responsible for the uptake of resource with efficiency α . The other species 'feed off' this primary producer either by grazing, predation or uptake of waste.

C. Multicellular organisms

We now consider more complex organisms that are multicellular. All the organisms live in an ecosystem and are connected to the primary producers by the flow of resource, either directly or indirectly by predation, or both. It is now possible to distinguish types of organism and we will label the different types or categories distinguished in this way with index p . Again, the results to follow will not depend upon the precise details of how individuals are assigned to any of the p categories, simply that such an assignment can be made. Different methods for categorizing the individuals in an ecosystem [23] will organize individuals into groups or categories of different p , this categorization may focus on the functional role of individuals in the ecosystem such as niche or trophic level, or may focus on stage of development, or other factors. Organisms falling into a given p^{th} category or group will be clustered around an average body size, on average they will be composed of $B(p)$ cells (this is typically observed [4]), and will have average metabolic rate $RB(p)$, the per-cell metabolic rate R now corresponds to an ecosystem average over these multicellular organisms. There is a non-trivial correspondence between average size $B(p)$ and how complex an organism can be. Within each p there will be a number $k = 1..S(p)$ of differentiable species each with density $n(k, p)$ all with average body size $B(p)$ and with average density, for that p of

$$\bar{n}(p) = \langle n(k, p) \rangle_k = \frac{1}{S(p)} \sum_{k=1}^{S(p)} n(k, p) \quad (5)$$

Our relevant variables of density and diversity now relate to the observation of a given category p_* that is embedded in the ecosystem; we observe $n_* = \bar{n}(p_*)$, $S_* = S(p_*)$. Individuals in the observed category also has a characteristic average size $B_* = B(p_*)$ (number of cells so dimensionless) which introduces an additional variable giving a total of 7 variables and hence 4 dimensionless parameters:

$$\Pi_1 = \frac{\alpha PL^2}{R}, \Pi_2 = n_* L^D, \Pi_3 = S_*, \Pi_4 = B_* \quad (6)$$

The physical constraint of a dynamically balanced ecosystem is now:

$$\frac{\alpha PL^2}{R} = \sum_p \sum_{k=1}^{S(p)} n(k, p) B(p) L^D = \sum_p \bar{n}(p) S(p) B(p) L^D \quad (7)$$

We can write (7) in terms of our observed p_*^{th} category:

$$\frac{\alpha PL^2}{R} = n_* S_* B_* L^D \sum_p \frac{\bar{n}(p) S(p) B(p)}{\bar{n}(p_*) S(p_*) B(p_*)} \quad (8)$$

We then have an expression of the form:

$$\frac{\alpha PL^2}{R} = n_* S_* B_* L^D \Psi(p_*) \quad (9)$$

where $\Psi(p_*)$ is a dimensionless function; $1/(\Psi(p_*))$ is the fraction of the total rate of resource supplied to the ecosystem that is utilized by the observed (p_*^{th}) category. Importantly, all of the species and categories are connected into the same resource flow, so that fundamentally, (9) will constrain how observed density, diversity and body size are related to each other across the ecosystem, with consequences for macroecological patterns as we will discuss.

These dimensionless parameters (6), and their relationship (9) express the following fundamental properties of the idealized ecosystem. There is a building block on which life is organized- the single cell which has a definable typical metabolic rate, R . There is then the physical property of resource flow: that the single cell metabolic rate, along with the rate of uptake of resource to the ecosystem αPL^2 constrains the number of cells the ecosystem can support, which is Π_1 . The detailed biological and ecological properties of the ecosystem then organise these Π_1 cells into a complex network of species and groups of species, observationally these are characterized into functional units which have an average body size, density and diversity. Hence, the observed ecological variables are in a macroscopic sense related to each other by the physical property of resource flow.

D. Non uniform distribution of individuals in space.

Generally, organisms will not be uniformly distributed in space so that the density depends on the length scale

r over which it is observed, so that $n = n(r, k, p)$ and similarly, the efficiency of the primary producers, which depends on their density, is $\alpha = \alpha(r)$. The lengthscale over which the density varies can either arise from how individuals subdivide and grow, forage, or other forms of influence they have on each other and on the environment. This is important since in (7-9) the density refers to that measured over the habitat of the entire ecosystem on scale L and any observation will be on a more local scale $r \ll L$, which in turn relates to the lengthscale of over which the density varies. This will introduce a variable for the scale of observation of the p^{th} category; r_* (dimension $[L]$) finally giving 8 variables so 5 dimensionless parameters:

$$\Pi_1 = \frac{\alpha_* PL^2}{R}, \Pi_2 = n_* L^D, \Pi_3 = S_*, \Pi_4 = B_*, \Pi_5 = \frac{r_*}{L} \quad (10)$$

where $\alpha_* = \alpha(r_*)$ so that all variables refer to a consistent set of observations on lengthscale r_* . The observed density can be generally expressed as $n(r, k, p) = n(L, k, p)/g(k, p, r/L)$ where g is dimensionless; similarly $\alpha(r) = \alpha(L)/g_\alpha(r/L)$. If the categorization p is based on function and structure then one can anticipate that an average of g over the $S(p)$ species in the category is meaningful so that

$$\begin{aligned} \bar{n}(r, p) &= \langle n(r, k, p) \rangle_k = \frac{1}{S(p)} \sum_{k=1}^{S(p)} n(r, k, p) \\ &= \frac{1}{S(p)} \sum_{k=1}^{S(p)} \frac{n(L, k, p)}{g(k, p, r/L)} = \bar{n}(L, p)/\bar{g}(p, r/L) \end{aligned} \quad (11)$$

With notation $g_* = \bar{g}(p_*)$ expression (9) becomes, for the observed p_* :

$$\begin{aligned} \frac{\alpha(L)PL^2}{R} &= \sum_p \bar{n}(L, p)S(p)B(p)L^D \\ &= \sum_p \bar{n}(r, p)\bar{g}(p, r/L)S(p)B(p)L^D \\ &= n_* S_* B_* g_* \left(\frac{r_*}{L}\right) L^D \sum_p \frac{\bar{n}(p)\bar{g}(p, r/L)S(p)B(p)}{\bar{n}(p_*)\bar{g}(p_*, r_*/L)S(p_*)B(p_*)} \end{aligned} \quad (12)$$

or writing the spatial variation in a single function $G(r/L) = \bar{g}(r/L)/g_\alpha(r/L)$

$$\frac{\alpha_* PL^2}{R} = n_* S_* B_* G\left(\frac{r_*}{L}\right) L^D \Psi(p_*) \quad (13)$$

Spatial variation in density thus leads to spatial trends in diversity, or species- area rules; this has arisen quite generally as a consequence of the physical constraint (13) and we will discuss this next.

Essentially, (13) is:

$$\Pi_1 = \Pi_2 \Pi_3 \Pi_4 G(\Pi_5) \Psi(p_*) \quad (14)$$

The dimensionless functions Ψ and G capture all the details of the ecosystem function and reflect how complex the ecosystem is. The level of complexity that an ecosystem can support increases with the number of different possible configurations that are possible and this is constrained by the number of cells the ecosystem can support. For example, if there is only one distinguishable kind of organism in the ecosystem, there is only one p and S value and $\Psi = 1$, we essentially recover (2) where the average metabolic rate of the organisms is RB_* . The threshold for one such organism to be supported by the ecosystem is $\Pi_1/\Pi_4 = 1$ or $\alpha_* PL^2/(RB_*) = 1$. As the ecosystem becomes more complex, $\Psi > 1$ and each p category utilizes a smaller share of the total resource supplied. The dimensionless function Ψ thus operates as an order parameter of the ecosystem which reflects the level of complexity. The corresponding control parameter is Π_1 . A physical analogy to this is the relationship between the Reynolds number in turbulence and the number of excited modes or degrees of freedom. The Reynolds number is the ratio of a rate of energy input on the largest, driving scale to a rate of energy dissipation on the smallest scale, as is Π_1 here, and dimensional analysis, along with the assumption of steady state (no energy pile up) is sufficient (see eg [22]) to constrain the number of degrees of freedom to grow with increasing Reynolds number.

III. CONSTRAINTS ON MACROECOLOGICAL PATTERNS WITHIN AND ACROSS ECOSYSTEMS

Observations both within and across ecosystems consist of specifying a method for classifying individuals into particular groups or categories and then for each of the p^{th} categories, observing the average density, diversity, bodysize, and metabolic rate. From the constraint (13) we see that these variables are not independent, and (13) suggests relationships between them which we will now discuss.

Let us consider that a scheme for classifying individuals is consistently adopted, and observations of average density, diversity, bodysize, and metabolic rate of these categories are made. These observations simultaneously collect a range of values of n_*, S_*, B_* for a given r_*, L and P . We will first consider the case where 'similar' ecosystems are compared, or where a comparison is made within a single ecosystem, that is, the order parameter Ψ is not varying. Subsets of the variables in equation (13) will then show functional relationships provided that the remaining variables do not strongly vary, this has been found for example by [24, 25] who demonstrate a relationship between species richness, area and a measure of productivity.

If one variable dominates our expression and Ψ is held constant (13) predicts the following patterns or trends:

- *Diversity and Wright's Rule:* $S_* \propto \alpha PL^2$, so that the number of species (diversity) increases with

total net productivity integrated over the habitat rather than productivity alone; this is Wright's rule [26]. Whilst Wright's rule is to some extent ecologically trivial (a greater net energy input allows more individuals, see [27]) the interesting aspect of this result is that it predicts an increase in diversity (richness) and not just individuals. As we would anticipate from (13) the relationship between productivity and species diversity also varies with spatial scale as is found [28].

- *Diversity and metabolic rate:* $S_* \propto 1/R$ so that diversity decreases with increasing metabolic rate: we expect ecosystems dominated by endothermic organisms with high metabolic rate to have lower diversity than those dominated by ectothermic, low-metabolism, organisms (e.g. [4]).
- *Latitudinal gradient rule:* For fixed metabolic rate, habitat size, and so on, diversity will increase with resource. Provided that other factors that link resource uptake to available sunlight do not vary [27] our general macroecological relationship encapsulates the latitudinal gradient rule. Again, this trend is present alongside patterns in the other variables in (13) as discussed by [29]. For example, (13) predicts that low metabolic rate ecosystems where the rate of resource supply is high will be more diverse than high metabolic rate ecosystems where the rate of resource supply is low; this may suggest a refined version of the latitudinal gradient rule.
- *Species Area Relationships:* A corollary of length-scale dependence of the density is that $S_* \propto L^{2-D}/G_*(\frac{r_*}{L})$ that is, diversity will vary both with habitat size (which is a function of L) and the lengthscale of the observation or characteristic lengthscale of some process lengthscale (which is a function of r_*); these are known as Species Area Relationships (SAR) (see eg [30]). Thus if the individuals grow in clumps, say by division, or live on a fractal structure (tree, coral, mountain, river) or forage in a random walk pattern (13) will constrain the resulting ecosystem SAR. For example power law SAR arise if available productive surface area or volume orders the availability and uptake of resource [31] and that this is in turn ordered by the roughness of the terrain which can be modeled simply as a fractal [32, 33], see also [34]. Within a given ecosystem, diversity and abundance will both vary with the r_* over which they are observed, as well as with each other. If all other variables are not strongly varying, their functional dependence on r_* can be obtained from the data by the method of scaling collapse as has been done by [35]. Again, these SAR and the underlying constraint on dispersal and clumping from which they originate will also be found to interact with other variables such as productivity [36] and bodysize [37]. Observations over the largest regional or continental scales

tend to integrate or aggregate over detailed spatial dependence and over other variable factors such as metabolic rate. These scales exceed that over which the terrain varies, and over which processes occur that yield spatial clumping, over such large scales the effective $G \rightarrow 1$ and the landscape is essentially 'flat' so that $D = 2$. Hence on these largest scales the spatial dependence in (13) vanishes, we have that $P \sim S_*$, and positive relationships between productivity and diversity emerge as has been found [28].

- *Abundance, the 'more individuals' hypothesis:* The number of individuals in a species $n_* L^D \propto \alpha P L^2 / R$ so that abundance (density of individuals in each species) increases with productivity integrated over the habitat and decreases with the typical metabolic rate (e.g. [4]). As we increase the total ecosystem energy take up rate, from equation (13) both the diversity and abundance can increase (for fixed metabolic rate). We will find the above patterns when one effect does not dominate, for example, Wright's rule will not be seen if the increase is entirely in abundance, and not in diversity. The relationship between the number of individuals and the number of species has long intrigued ecologists, and whilst a positive relationship is sometimes assumed (the 'more individuals' hypothesis for the increase in richness with overall abundance: see [27]) the mechanism(s) involved are far from clear.
- *Abundance, diversity and body size:* $B_* \propto 1/(n_* S_*)$ so that the average abundance [38–42] and diversity [4] are found to have statistical trends that decrease with increasing average body size.
- *If body size trends correspond to trends in trophic level* then since $B_* \propto P L^D / R$ the number of trophic levels that the ecosystem can support increases with total net productivity summed over the habitat and decreases with the typical metabolic rate [4]. Alternatively the number of trophic levels for example may be determined by the level of complexity Ψ which increases with total net productivity summed over the habitat and decreases with the typical metabolic rate.

Our result, equation (13), identifies a functional relationship between ecosystem variables. It also immediately suggests why many such patterns show considerable variability; for example, plotting abundance versus body size does not eliminate other dependencies such as on metabolic rate, diversity and the rate of supply of resource. We now use (13) to identify a method to isolate these patterns.

IV. NORMALIZING TO TEST FOR PATTERNS WITHIN AND ACROSS ECOSYSTEMS

As a starting point say we have a set of observations based on individuals consistently organized into categories. For each category we observe on lengthscale r_* the density n_* , diversity S_* and body size B_* , so that for many such categories we have a set of observations of n_* , $[n_1, n_2, \dots, n_j, \dots]$, of S_* , $[S_1, S_2, \dots, S_j, \dots]$, and of B_* , $[B_1, B_2, \dots, B_j, \dots]$ where each n_* and S_* refer to size B_* of the p_*^{th} category. We first consider the case where these are all drawn from the same ecosystem and observed on the same lengthscale so that we have the same α, P, L, R, G and r^* . There will be a single function $\Psi(p_*)$ which corresponds to this set of observations at different p_* . We can write

$$\Psi(n_* S_* B_*) = \frac{n' S' B'}{n_* S_* B_*} \Psi(n' S' B')$$

so that relative to any particular category $n' S' B'$ we can obtain $\Psi(n_* S_* B_*)$ to within a constant. Alternatively one can treat p_* as a parametric coordinate, and obtain the trend with any one of n_*, S_*, B_* .

This procedure is illustrated in Figure 1 where we have modelled synthetic data. Our synthetic data are generated such that there are trends in abundance, diversity and body size, and also random scatter in all variables. Importantly this random scatter is generated to be constrained such that all the sampled categories of individuals share the same function Ψ ; the plots show that this constraint only emerges in a plot of $1/S_* n_* B_*$ versus body size B_* . This also offers a method to compare different categorization schemes which for the same ecosystem could yield different $\Psi(p)$; one could then in principle normalize for (ie compensate for) any 'bias' introduced by a particular choice of categorization.

Practically, data is obtained across ecosystems as well as within them so that now α, P and L may vary. A particular example of this is testing for SAR. To test for a SAR one should plot the normalized diversity \bar{S} :

$$\bar{S} = \frac{S_* n_* R B_* \Psi(p_*)}{\alpha_* P} = \frac{L^{2-D}}{G(r_*, L)} \quad (15)$$

versus L with $\Psi(p_*)$ found as above, or a comparison made such that $\Psi(p_*)$ is not strongly varying ('similar' ecosystems).

We illustrate this process in Figure 2 where we have modeled synthetic data for a species-area comparison. We have generated synthetic data in the same manner as in Figure 1, such that there are trends in abundance, species richness, and body size, and also random scatter in all variables, constrained such that all the sampled categories of individuals share the same function Ψ . In addition each group of data is from a different habitat size and has a dependence on area predicted by our result (13) with power law dependence of G on L . This clear pattern in normalized diversity has a corresponding SAR

pattern of diversity versus area which has considerable scatter

V. CONCLUSIONS

We have used a 'bottom up' approach to fix the minimum set of variables needed to specify a generic idealized ecosystem. Physical constraints of energy flow and utilization over the ecosystem, and dimensional constraints, then relate the level of complexity that the ecosystem can support to intrinsic variables such as density, diversity and characteristic lengthscales for foraging or dispersal, and extrinsic variables such as habitat size and the rate of supply of resource. These constraints hold regardless of the details of how a given ecosystem functions and require only three key assumptions, (i) that the ecosystem is in a dynamically balanced steady state, (ii) that some (non- unique) method can differentiate different functional groups of individuals within the ecosystem and (iii) that these functional groups are connected to each other by the flow of resource. We thus find the constraint on the relationships that can exist between these (dimensional) ecosystem variables which is reflected in observed macroecological patterns. Our result may explain why these general, approximate statistical trends appear to be so ubiquitous in nature: we obtain these patterns without recourse to any detailed information about the structure or dynamics of ecosystems or indeed how the data is collected.

Our result fixes the relationship between ecosystem variables. This leads to the dimensionless, or normalised variables that need to be constructed to isolate the trend in one ecosystem variable from another; this provides a new method for isolating macroecological patterns. Comparisons could thus be made between datasets by controlling for (normalizing against) characteristic metabolic rate, abundance and diversity in order to isolate the statistical pattern with respect to one of these variables. In particular this method isolates a function that expresses how complex the ecosystem is and it would be intriguing to order the data in this way to determine the level of complexity of ecosystems that are found in nature, and to what conditions they correspond. An example would be comparisons across extinct ecosystems, or between extinct and contemporary ecosystems, provided a comparable sample group could be identified. The fact that Wright's rule, species area rules and latitudinal gradient rules emerge often, but not always, from the observational data gathered across ecosystems may reflect varying levels of complexity in these ecosystems, or the effect of different schemes for categorizing individuals within ecosystems and our results provide a method to control for this.

Departures from these statistical patterns where ecosystems are similar, and consistently sampled, then imply that the system is in a state of rapid change, i.e., abundance or diversity explosion or collapse. Any ecosys-

tem which is dynamically balanced in the sense discussed above will fall within these macroecological patterns, it does not need to be a climax or maximum energy utilization system but simply needs to balance the rate of energy uptake with that of usage integrated over the ecosystem.

Finally, we have identified a dimensionless control parameter for ecosystem density and diversity, namely $(\text{productivity}) \times (\text{habitat size}) / (\text{typical metabolic rate})$ which quite generally emerges from our dimensional analysis. This we suggest will be a control parameter in dynamical models for ecosystems based on energy flow and conservation and will order the emergent behaviour of these models. We relate this control parameter to the level of complexity that a dynamically balanced ecosystem can support (its order parameter). This control parameter is the ratio of energy input rate to the ecosystem

to the metabolic rate of the smallest possible unit of life, a single cell. If it is reasonable to identify a smallest possible unit of life then this parameterizes the threshold at which life, defined in this manner, can occur (c.f. Lovelock's conjecture about dimensionless control parameters for prebiotic planets [43]).

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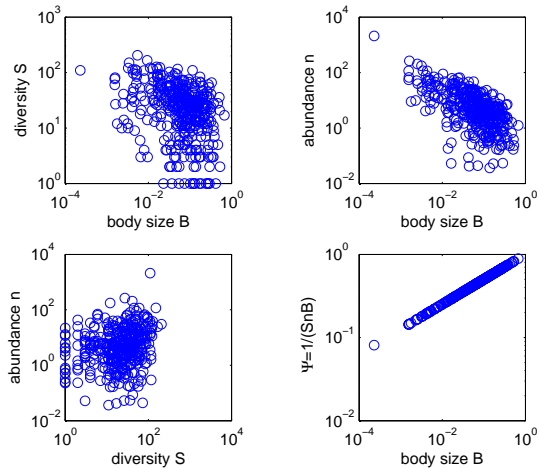


FIG. 1: Log-log plots of synthetic data generated for an ecosystem where all the observed individuals are constrained to share the same ecosystem complexity function Ψ . The data is constructed to show trends in abundance, diversity and body size with random scatter. The constraint can only be discerned by plotting $1/S_j n_j B_j$ versus body size B_j .

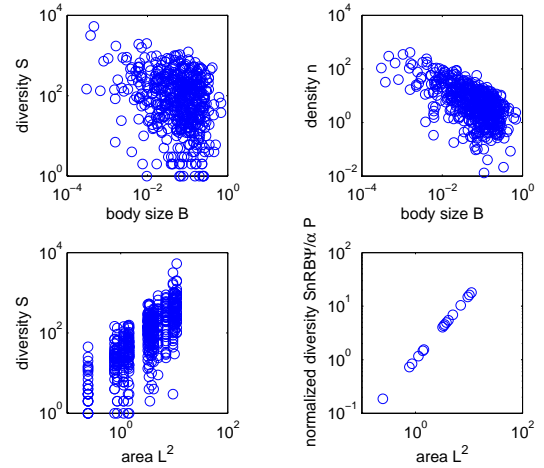


FIG. 2: Log-log plot of synthetic data generated for categories of individuals from habitats of different areas. The data is constructed with power law dependence of diversity on lengthscale and trends in abundance, diversity, body size and area with random scatter. This pattern is only revealed in a plot of dimensionless diversity versus area.